

Controls on soil respiration in semiarid soils

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Abstract

Soil respiration in semiarid ecosystems responds positively to temperature, but temperature is just one of many factors controlling soil respiration. Soil moisture can have an overriding influence, particularly during the dry/warm portions of the year. The purpose of this project was to evaluate the influence of soil moisture on the relationship between temperature and soil respiration. Soil samples collected from a range of sites arrayed across a climatic gradient were incubated under varying temperature and moisture conditions. Additionally, we evaluated the impact of substrate quality on short-term soil respiration responses by carrying out substrate-induced respiration assessments for each soil at nine different temperatures. Within all soil moisture regimes, respiration rates always increased with increase in temperature. For a given temperature, soil respiration increased by half (on average) across moisture regimes; Q_{10} values declined with soil moisture from 3.2 (at -0.03 MPa) to 2.1 (-1.5 MPa). In summary, soil respiration was generally directly related to temperature, but responses were ameliorated with decrease in soil moisture.

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1. Introduction

Global soil respiration is estimated to be 76.5 pg C per year which is 30–60 pg C per year greater than global net primary production (Raich and Potter, 1995) and is thus a very substantial flux in the global C cycle (Schimel, 1995). Reviews of laboratory-based soil respiration measurements have found that the soil respiration increases with temperature. Rates of response, quantified using a Q_{10} relationship, are inversely related to temperature (Kirschbaum, 1995; Lloyd and Taylor, 1994): soils from colder climates are more sensitive to increases in temperature. This relationship between soil respiration and temperature has been successfully incorporated into a number of soil organic matter models (e.g. Century and Roth C, Jenkinson and Rayner, 1977; Parton et al., 1987). While some aspects of temperature controls on soil respiration have recently been questioned (Giardina and Ryan, 2000; Holland et al., 2000), it is clear that soil respiration responds

positively to temperature in a number of systems and that temperature is just one of a host of variables that influences soil respiration (Davidson et al., 2000).

Field-based soil respiration measurements demonstrate that Q_{10} values for soil respiration can vary spatially (Conant et al., 1998) and seasonally (Borken et al., 1999; Davidson et al., 2000) and are related to the distribution of soil moisture. Soil moisture can influence soil respiration for all or part of the year particularly in arid or semiarid ecosystems (Amundson et al., 1989; Conant et al., 2001), but also in more mesic systems (Borken et al., 1999; Davidson et al., 1998; Gardenas, 2000; Savage and Davidson, 2001). Soil moisture can limit soil respiration by limiting microbial contact with available substrate and dormancy and/or death of microorganisms at low soil water potentials (Orchard and Cook, 1983). Arid and semiarid lands (areas where precipitation exceeds annual potential evapotranspiration) comprise more than one-third of the earth's surface (Koppen, 1954) and it is likely that temperature-driven increases in soil respiration are dampened by low soil moisture for part or all of the year in these areas (Raich and Potter, 1995). The purpose of this

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work was to evaluate the influence of soil moisture on the relationship between temperature and short-term microbially-mediated soil respiration rates. Soils from a series of semiarid sites, situated along an elevation gradient, with different soil C contents, vegetative communities, microbial communities (i.e. fungal vs. bacterial populations), mean annual temperatures, and mean annual precipitation were incubated under a range of independently varying temperature and moisture conditions. The interplay of these four controlling factors (temperature, moisture, microbial community structure, and soil C) were evaluated in order to better understand (1) moisture-driven limits to the positive relationship between temperature and soil respiration and (2) variability of respiration responses to increased temperature across a range of temperatures.

2. Materials and methods

The research area is located in the Coconino National forest, due north of Flagstaff, Arizona on the leeward side of the San Francisco mountains between 35°25'N, 111°34'W and 35°26'N, 111°40'W. The area covers a 7 km transition zone with great basin desert scrub (DS) at the lower elevation, pinyon–juniper woodlands (PJ) in the middle, and ponderosa pine (PP) forest at the upper elevation. The DS site is dominated by winterfat (*Ceratoides lanata* (Pursh) Moq.), snakeweed (*Gutierrezia sarothra* (Pursh) Britt. and Rusby), rubber rabbit brush (*Chrysothamnus nauseosus* (Pall.) Britton.) and blue grama grass (*Bouteloua gracilis* (H.B.K.) Lag.). The PJ site contains one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.) and pinyon pine (*Pinus edulis* Engelm.), with blue grama dominant in interspaces. The PP site is an open, park-like stand of PP (*Pinus ponderosa* Doug. ex Laws.) with mutton grass (*Poa fendleriana* (Steud.) Vasey), mountain muhly (*Muhlenbergia montana* (Nutt.) Hitchc.) and buck brush (*Ceanothus fendleri* Gray.) in the understory.

Soils at all sites were derived from volcanic material and are classified as Typic Haplustolls at the DS site grading into Aridic Argiustolls at the PJ site and Typic Argiborolls at the PP site. Soils are all sandy loams and are basic (pH = 7.5) to slightly acidic (pH = 6.6). Mean annual temperatures based on 30 years of climatic data range from 8.5 °C at the DS site to 5.5 °C at the PP site and mean annual precipitation ranges from approximately 320 mm per year at the DS site to 530 mm per year at the PP site (Klopatek et al., 1998) (Table 1).

Four replicate mineral soil samples, consisting of surface (0–15 cm) composites from six locations, were collected in early march (just after snowmelt) from randomly located interspace locations at each of the three sites and from underneath four randomly selected canopies of each tree type (pinyon and juniper canopies at the PJ site; PP canopies at the PP site). Samples were sealed in plastic bags, returned to the lab at field moisture, and stored under refrigeration

Table 1

Site characteristics for the three sites from which soils were collected for this experiment from Klopatek et al. (1998)

Site	Mean annual temperature (°C)	Mean annual precipitation (mm)	Elevation (m)
Desert scrub (DS)	8.5	310	1987
Pinyon–juniper (PJ)	7.1	410	2126
Ponderosa pine (PP)	5.5	530	2295

(4 °C). Samples were passed through a 2 mm sieve to remove rocks and coarse roots; finer roots were then hand picked from each sample. Gravimetric soil moisture was determined on a 20 g subsample by oven drying at 70 °C for 24 h. Soil pH was measured in a 1:1 soil to 0.01 M CaCl₂ solution. Soil texture, was determined using the hydrometer method and soil C and N contents were determined on a Perkin–Elmer 2400 CHN Autoanalyzer (Perkin–Elmer, St Joseph, MO).

Water potential was determined on all soil samples using a pressure plate apparatus. Soil samples (25 g) contained in metal rings with fine mesh bases were wet to field capacity and exposed to increased atmospheric pressure. Samples were allowed to equilibrate for 24 h at each pressure increment (–0.03, –0.50, –1.00, and –1.50 MPa) and were then weighed to determine water holding capacity at each pressure. Sterile nanopure water was injected into the soil samples to bring them to the proper soil moisture. If soil moisture content was greater than soil water content desired for incubations, the soil was air dried for 24 h and sterile nanopure water was added back to the soil to establish the proper soil moisture content (Table 2).

Bulk soil incubations were performed using 50 g of each replicate soil sample in 500 ml sealed glass jars topped with rubber septa. Soils were incubated at four temperatures (5, 15, 15, and 35 °C) maintained by water baths and constant temperature chambers, and four water holding capacities (–0.03, –0.50, –1.00, and –1.50 MPa). Headspace CO₂ concentration was determined initially and after 5 days of incubation by collecting a 100 µl sample of headspace gas from each jar using a 500 l gas-tight, locking syringe (Hamilton, Reno Nevada) and analyzed using a gas chromatograph. CO₂ concentration of headspace gas samples was determined using a Perkin–Elmer Sigma 2000 gas chromatograph with a thermal conductivity detector fitted with an Alltech 6 ft × 1/8 in. stainless steel 80/100 mesh Poropak Q column. Nitrogen was the carrier gas at 30 ml min^{–1}. The injector, detector, and column were set at 150, 225, and 50 °C, respectively. A jar without soil served as a CO₂ blank. Soil respiration was assumed to equal the change in CO₂ concentration over the incubation period minus the changes in concentration in the blanks.

Table 2
Soil texture and soil moisture at field capacity for the six soils used in this experiment

Soil	Cover type	Sand (%)	Silt (%)	Clay (%)	Water holding capacity (g H ₂ O g soil ⁻¹)	Soil C (kg C ha ⁻¹)	C:N
DS-I	Interspace	70.7	15.6	13.7	0.16	10.5	10.5
PJ-I	Interspace	63.7	13.6	22.7	0.22	11.9	9.2
PJ-J	Juniper canopy	72.6	13.6	13.8	0.16	17.9	12.8
PJ-P	Pinyon canopy	66.1	12.6	21.3	0.17	15.8	11.3
PP-I	Interspace	69.7	12.3	20.0	0.14	12.3	17.6
PP-PP	Ponderosa pine canopy	69.7	12.7	17.6	0.21	16.2	20.3

Soil names refer to the site and cover type of origin.

Substrate-induced (SI) respiration rates were performed to evaluate impacts of substrate quality on short-term soil respiration responses to temperature. Three replicate soil samples (2.5 g wet wt.) were added to 40 ml vials sealed with teflon-lined silicon septa. Sterile nanopure water was added to give a final ratio of 2:1 on a dry weight basis. Filter sterilized (0.2 mM) D-glucose was then added from a 1 M stock solution to give a final concentration of 20 mg ml⁻¹; 0.5 mg was added to each gram of soil. This concentration demonstrated to saturate respiratory activity in these soils within the time frame of these experiments. The vials were then laid horizontally in a reciprocating water bath (180 rpm) and incubated at the respective temperatures (4, 10, 15, 20, 26, 30, 35, 40, and 45 °C) for 30 min at which time 100 µl of the headspace was sampled and injected into the gas chromatograph. A second sample was taken 1–2 h later to determine the respiration rate. Optimization experiments demonstrated that the rate of CO₂ evolution was linear in this time frame.

All analyses were carried out on field replicates. Differences between incubation temperatures and moistures

were compared statistically using one-way analysis of variance and Scheffe's means comparison test in SAS (SAS, 1985). Soil respiration quotients (Q_{10} s) for bulk soil incubations and SIR incubations were determined by dividing the difference in soil respiration rates for two incubation temperatures by the difference in incubation temperature. Reported Q_{10} values are averages across all (positive) increments.

3. Results

Soil respiration rates for DS soils ranged from 2.9 to 61.4 µg CO₂-C mg soil C⁻¹ d⁻¹. Within all water potentials, respiration rates always increased with increase in temperature (Fig. 1). Soil respiration rates under the warmest incubation temperatures averaged four fold more than those under the driest conditions; the largest difference (nearly eight fold) occurred in the wettest soil (Fig. 1). Across all incubation temperatures soil respiration increased to an average of 72% between moisture classes.

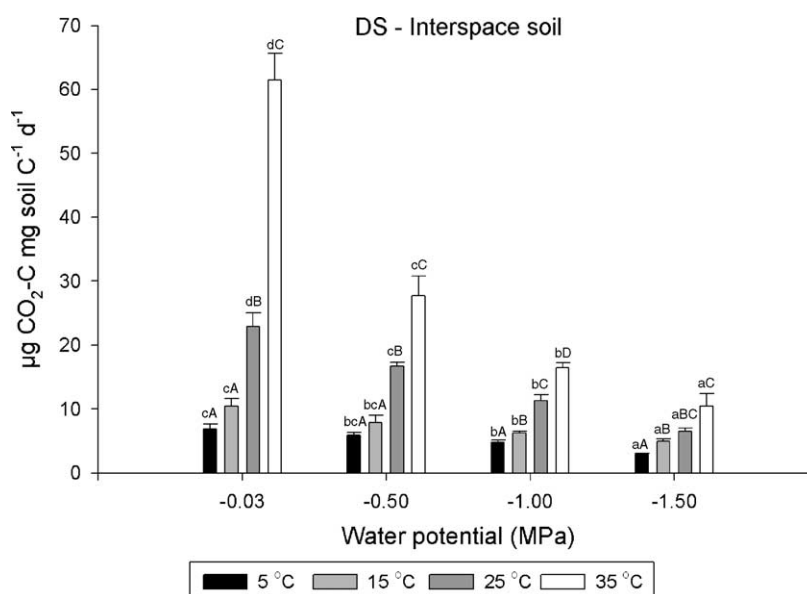


Fig. 1. Soil respiration for soils from the desert scrub (DS) site incubated under four temperatures and four soil moisture contents. Different lower case letters indicate significant ($P < 0.05$) differences between samples incubated under similar temperatures but different soil moisture contents. Different capital letter indicate significant ($P < 0.05$) differences between samples incubated under similar soil moistures, but different temperatures.

Soil respiration rates were significantly ($P < 0.05$) greater in the wetter soils (-0.03 and -0.50 MPa) than in the two driest soils with the exception of the difference between the soils incubated under -0.03 and -0.50 MPa at 5 and 15 °C (Fig. 1). On average, soil respiration was 2.5 times greater under the wettest incubation conditions than under the driest conditions and increased to an average of 50% across all one-step moisture increases. Soil respiration rates decreased with decreasing water potential with all incubation temperatures (Fig. 1).

Responses to different incubation temperatures and moisture contents at the PJ site were similar to those at the DS site (Fig. 2). The range of soil respiration rates observed for interspace soils collected from the PJ site (5.6 – 47.8 $\mu\text{g CO}_2\text{-C mg soil C}^{-1} \text{d}^{-1}$) was narrower than that observed at the DS site. Rates for soils collected

under canopies at the PJ site averaged 80% greater than those from interspaces across all treatments. Soil respiration rates for soils collected under canopies ranged from 6.1 to 135.0 $\mu\text{g CO}_2\text{-C mg soil C}^{-1} \text{d}^{-1}$. Soil respiration rates tended to be greatest at the 25 °C incubation temperature. The difference in soil respiration rates for soils incubated at 15 – 25 °C tended to be greatest under wetter conditions at all three sites, with differences for the pinyon canopies most pronounced (Fig. 2a–c). Soil respiration tended to increase with increase in soil moisture for all soil types. Differences in soil respiration rates between different moistures were significant, ($P < 0.05$) more consistently for soils incubated under warmer temperatures, though the wettest soils (-0.03 and -0.05 MPa) usually had higher respiration rates than the drier (-1.00 and -1.50 MPa) soils (Fig. 2a–c).

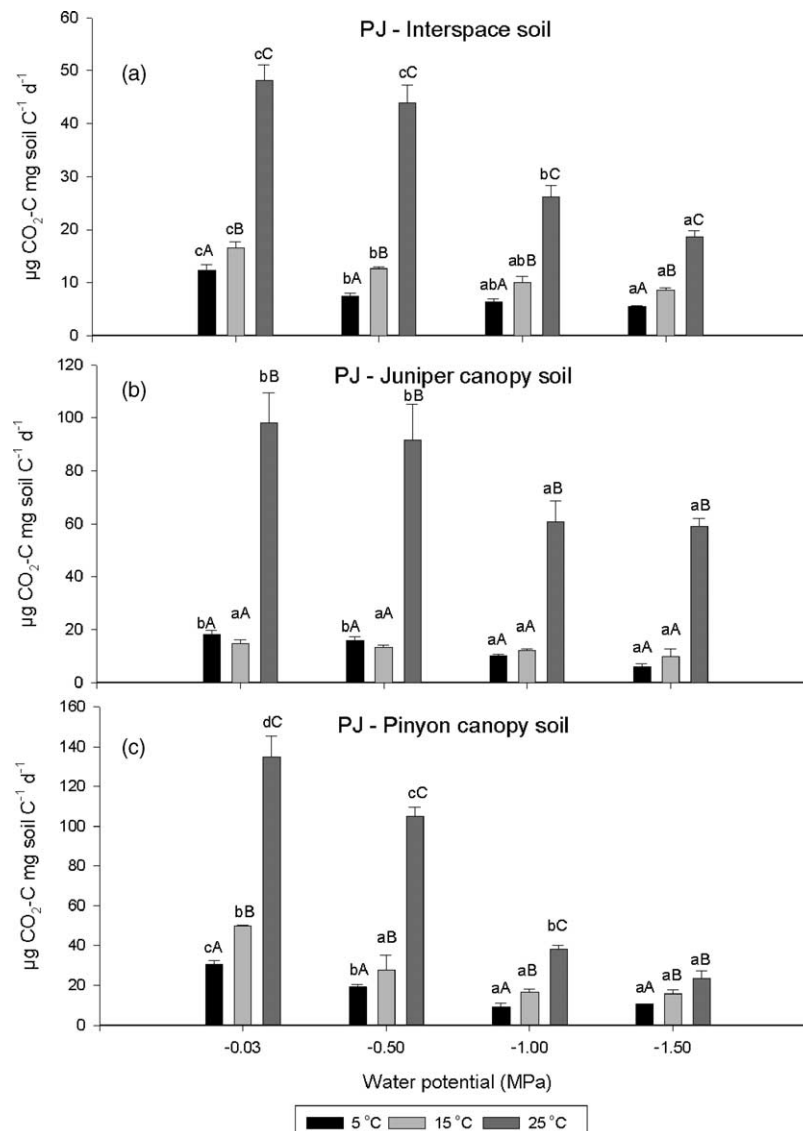


Fig. 2. Soil respiration for soils from the pinyon–juniper (PJ) site incubated under four temperatures and four soil moisture contents. Different lower case letters indicate significant ($P < 0.05$) differences between samples incubated under similar temperatures but different soil moisture contents. Different capital letter indicate significant ($P < 0.05$) differences between samples incubated under similar soil moistures, but different temperatures.

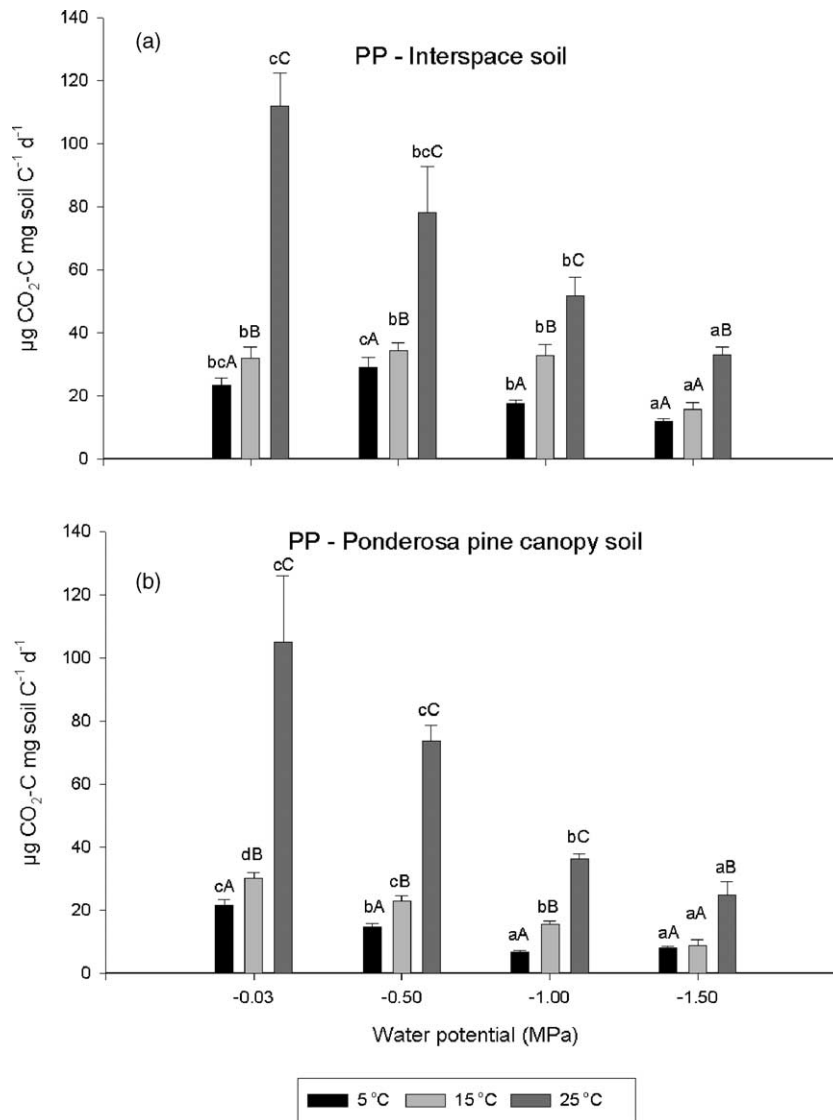


Fig. 3. Soil respiration for soils from the PP site incubated under four temperatures and four soil moisture contents. Different lower case letters indicate significant ($P < 0.05$) differences between samples incubated under similar temperatures but different soil moisture contents. Different capital letter indicate significant ($P < 0.05$) differences between samples incubated under similar soil moistures, but different temperatures.

Trends observed at the PP site were similar to those at the PJ site (Fig. 3). Soil respiration tended to be greatest for soils incubated at 25 °C, though differences were significant ($P < 0.05$) for canopy soils only for the driest soils (Fig. 3b). Soils incubated at 5 °C had significantly ($P < 0.05$) lower respiration rates than soils incubated at 15 °C (Fig. 3). Similar to the other sites, soil respiration tended to increase with soil water potential; rates were always significantly ($P < 0.05$) greater under the wettest soil moisture conditions (−0.03 MPa), and usually under the next wettest (−0.05 MPa), than the two driest incubation moisture conditions (−1.00 and −1.50 MPa).

Soil respiration quotients (Q_{10} values) were always significantly ($P < 0.05$) greater for the wettest soils than for the driest soils (Table 3). For the DS and PJ-interspace soils,

Table 3

Soil respiration quotients (Q_{10}) for soils incubated at four water potentials

Site	Cover type	Water potential (MPa)			
		−0.03	−0.50	−1.00	−1.50
DS	Interspace	2.78 (a)	1.95 (b)	1.61 (bc)	1.56 (c)
PJ	Interspace	2.90 (a)	2.67 (a)	2.66 (a)	2.28 (b)
PJ	Juniper canopy	4.32 (a)	4.52 (a)	2.68 (b)	2.52 (b)
PJ	Pinyon canopy	2.84 (a)	3.48 (ab)	3.89 (b)	1.66 (c)
PP	Interspace	3.16 (a)	2.01 (b)	2.03 (b)	2.01 (b)
PP	Ponderosa pine canopy	3.17 (a)	3.19 (a)	3.26 (a)	2.30 (b)

Different letters indicate significant differences ($P < 0.05$) in Q_{10} values between different water potentials.

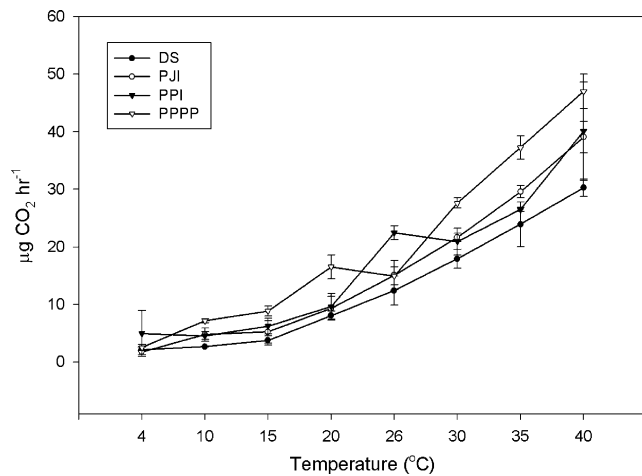


Fig. 4. Soil respiration rates for four soils incubated at eight temperatures.

Q_{10} values decreased with decrease in soil moisture. The highest Q_{10} values for the pinyon and juniper canopy soils at the PJ site and the ponderosa canopy at the PP site were observed under dried conditions (-0.50 , -1.00 , and -1.00 , respectively). Q_{10} values averaged across all soils decreased with soil moisture, ranging from 3.15 (at -0.03 MPa) to 2.06 (at -1.5 MPa). Averaged across all moisture contents, Q_{10} s at the DS site were lowest (1.97), and the interspace (2.80 and 2.31 for PJ-interspace and PP-interspace, respectively) soils were lower than the canopy soils at the other two sites (3.51, 2.99, and 2.98 for PJ-juniper, PJ-pinyon, and PP-ponderosa, respectively).

SI respiration rates increased with temperature for all four different soils (Fig. 4). SI respiration rates were significantly greater for the PP-ponderosa canopy soils than for the other three soils at six of the eight incubation temperatures; differences between all other soils at all temperatures were insignificant (Fig. 4). Soil respiration quotients were similar for all soils, ranging from 2.2 (PP-interspace) to 2.8 (PJ-interspace). Compared to Q_{10} s calculated from soil respiration rates for bulk soils, SIR Q_{10} s were similar for the DS-interspace and PJ-interspace soils, but were considerably lower than those for the PP-interspace and PP-ponderosa canopy soils.

4. Discussion

Results from this work support the hypothesis—derived from in situ field measurements (Conant et al., 1998) and experimental manipulations (Conant et al., 2001)—that soil respiration responses to increases in temperature are ameliorated at low soil moisture content. At low soil moisture content soil respiration was positively related to temperature for all soils, but responses were significantly smaller. Field studies in other locations have shown similar responses to increases in temperature under dry conditions,

but interpreting those results is complicated since temperature increases dry out the soil (Davidson et al., 1998). Likewise, a number of soil warming experiments have concluded that decreases in soil moisture concomitant with increases in temperature is a likely explanation for limited positive responses of soil respiration to increased temperature (e.g. Rustad et al., 2001). Our results demonstrate that soil respiration responses to increases in temperature are constrained by soil moisture for soils with a range of litter quality, soil textures, and microbial communities.

Soil respiration quotients from these incubations, ranging from 1.3 to 5.1, fall within the range of those studies reported elsewhere (Kirschbaum, 1995). Whereas other studies investigating soil respiration in laboratory incubations without water limitations have demonstrated a negative relationship between mean incubation temperature and Q_{10} response (Kirschbaum, 1995), our data follow the opposite trend. Q_{10} values at lower temperatures (5–15 or 15–25 °C for the DS soil) tended to be greater than those for warmer incubation temperatures; differences were smaller under dried incubation conditions. SI respiration Q_{10} values, however, did tend to decrease with increase in incubation temperature. Lack of agreement between these data suggests that decomposition of soil organic matter, which is more recalcitrant than the added substrate, requires overcoming higher activation energy.

It is interesting to note that, with the exception of the DS site, Q_{10} s averaged across all incubation moistures differed little between sites. We expected that poor litter quality at the higher elevation sites would lead to smaller differences in respiration rates between different temperatures and, thus, lower Q_{10} s. Bulk soil respiration independent of soil C (not shown) was lowest for the DS-interspace and PJ-interspace soils under all conditions indicating that these soils contain less easily decomposable material, suggesting that respiration responses to temperature may have been limited by soil C content. Gallardo and Schesinger (1992) demonstrated that in Chihuahuan desert soils as the ratio of C:N decreased, microbial biomass became limited by C, which may have been the case for the DS-interspace and PJ-interspace soils. Conversely, larger responses for the PJ-canopy and PP soils suggest that soil respiration in these soils is not C limited.

This research clearly demonstrates that soil respiration responses to changes in temperature will be a function of direct impacts on the activity of decomposers. Furthermore, these short-term responses will be impacted by soil moisture and microbial community characteristics and can be altered by soil C quality. Over the longer-term shifts in microbial community composition, changes in the amount, timing, and quality of litter inputs, and ultimately different soil C quality may drive changes in soil C formation and turnover. However, the results reported here corroborate field-based observations that soil respiration responses to increase in temperature appear to be constrained by low soil moisture.

Our results provide support for modeling approaches that use multiplicative temperature and moisture decomposition rate reducing functions (e.g. Parton et al., 1987) and have important implications for understanding global change impacts on C cycling since moisture stress/limitations occur across such a large portion of terrestrial ecosystems.

References

- Amundson, R.G., Chadwick, O.A., Sowers, J.M., 1989. A comparison of soil climate and biological activity along an elevational gradient in the eastern Mojave desert. *Oecologia* 80, 395–400.
- Borken, W., Xu, Y.J., Brumme, R., Lamersdorf, N., 1999. A climate change scenario for carbon dioxide and dissolved organic carbon fluxes from a temperate forest soil: drought and rewetting effects. *Soil Science Society of America Journal* 63, 1848–1855.
- Conant, R.T., Klopatek, J.M., Malin, R.C., Klopatek, C.C., 1998. Carbon pools and fluxes along an environmental gradient in Northern Arizona. *Biogeochemistry* 43, 43–61.
- Conant, R.T., Klopatek, J.M., Klopatek, C.C., 2001. Environmental factors controlling soil respiration in three semiarid ecosystems. *Soil Science Society of America Journal* 64, 383–390.
- Davidson, E.A., Belk, E., Boone, R.D., 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. *Global Change Biology* 4, 217–227.
- Davidson, E.A., Trumbore, S.E., Amundson, R., 2000. Soil warming and organic carbon content. *Nature* 408, 789–790.
- Gallardo, A., Schlesinger, W.H., 1992. Carbon and nitrogen of soil microbial biomass in desert ecosystems. *Biogeochemistry* 18, 1–17.
- Gardenas, A.I., 2000. Soil respiration fluxes measured along a hydrological gradient in a Norway spruce stand in south Sweden (Skogaby). *Plant and Soil* 221, 273–280.
- Giardina, C.P., Ryan, M.G., 2000. Evidence that decomposition rates of organic carbon in mineral soil do not vary with temperature. *Nature* 404, 858–861.
- Holland, E.A., Neff, J.C., Townsend, A.R., McKeown, B., 2000. Uncertainties in the temperature sensitivity of decomposition in tropical and subtropical ecosystems: implications for models. *Global Biogeochemical Cycles* 14, 1137–1151.
- Jenkinson, D.S., Rayner, J.H., 1977. The turnover of soil organic matter in some of the Rothamsted classical experiments. *Soil Science* 123, 298–305.
- Kirschbaum, M.U.F., 1995. The temperature dependence of soil organic matter decomposition, and the effect of global warming on soil organic C storage. *Soil Biology & Biochemistry* 27, 753–760.
- Klopatek, J.M., Conant, R.T., Francis, J.M., Malin, R.A., Murphy, K.L., Klopatek, C.C., 1998. Implications of patterns of carbon pools and fluxes across a semiarid environmental gradient. *Landscape and Urban Planning* 39, 309–317.
- Koppen, W., 1954. Classification of climates and world patterns. In: Trewartha, G.T., (Ed.), *An Introduction to Climate*, McGraw-Hill, New York, pp. 225–226.
- Lloyd, J., Taylor, J.A., 1994. On the temperature dependence of soil respiration. *Functional Ecology* 8, 315–323.
- Orchard, V.A., Cook, F.J., 1983. Relationship between soil respiration and soil moisture. *Soil Biology & Biochemistry* 15, 447–453.
- Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. *Soil Science Society of America Journal* 51, 1173–1179.
- Raich, J.W., Potter, C.S., 1995. Global patterns of carbon dioxide emissions from soils. *Global Biogeochemical Cycles* 9, 23–36.
- Rustad, L.E., Campbell, J.L., Marion, G.M., Norby, R.J., Mitchell, M.J., Hartley, A.E., Cornelissen, J.H.C., Burevitch, J., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126, 543–562.
- SAS, 1985. *SAS User's Guide: Statistics Version 5 Edition*, SAS Institute Inc, Cary, NC.
- Savage, K.E., Davidson, E.A., 2001. Interannual variation of soil respiration in two New England forests. *Global Biogeochemical Cycles* 15, 337–350.
- Schimel, D.S., 1995. Terrestrial ecosystems and the carbon cycle. *Global Change Biology* 1, 77–91.